Histological study of the median lingual dental plate of the Cretaceous fish †*Palaeonotopterus greenwoodi* (Teleostei: Osteoglossomorpha) from the Kem-Kem beds, Morocco

by

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Abstract. – We describe the histology of the lingual dental plate of an extinct Notopteridae, †*Palaeonotopterus greenwoodi,* from the Cenomanian Kem-Kem Beds in Morocco. The lingual dental plate is bulky. Its regular and more or less smooth crushing surface does not exhibit any teeth externally. The plate is composed of several superimposed layers of side-by-side teeth. The teeth are attached to each other by a small amount of cellular bony tissue that may contain some vascular canals. The teeth originate inside the plate in a large dental cavity where odontogenesis takes place. Then, new teeth move passively towards the crushing surface and thicken to reach a maximum of 1 mm in diameter and 2 mm in height. The teeth are likely worn down by crushing food. Thus, †*Palaeonotopterus greenwoodi* had true "coalesced teeth" that constituted a lingual chewing apparatus displaying a process of tooth renewal similar to that described in extant fish with durophagous diet, i.e. scarids, tetraodontids and the carangid fish *Trachinotus teraia*. We thus assume that †*Palaeonotopterus greenwoodi* was durophagous. The Kem-Kem levels that yielded the lingual dental plates also delivered abundant shells of molluscs and remains of crustaceans that might have constituted prey of this extinct fish.

Résumé. – Étude histologique de la plaque dentaire linguale du poisson crétacé †*Palaeonotopterus greenwoodi* (Teleostei : Osteoglossomorpha) du site de Kem-Kem au Maroc.

Nous décrivons la structure histologique des plaques dentaires linguales d'un Notopteridae fossile †*Palaeonotopterus greenwoodi* du Cénomanien du Maroc. Ces plaques dentaires sont massives avec une surface d'abrasion d'aspect homogène sur laquelle aucune dent n'est visible. La plaque dentaire linguale est constituée de plusieurs couches superposées de dents étroitement juxtaposées et soudées les unes aux autres par un peu de tissu osseux cellulaire vascularisé. Ces dents prennent naissance au cœur de la plaque dentaire dans une cavité profonde où s'effectue l'odontogenèse. Les jeunes dents migrent passivement vers la surface d'abrasion tout en s'épaississant pour atteindre leur taille fonctionnelle : au maximum 1mm de diamètre pour 2 mm de hauteur. Les dents sont usées au niveau de la surface d'abrasion par le passage et l'écrasement d'aliments durs. †*P. greenwoodi* possède donc de véritables "dents coalescentes" qui constituent un appareil pharyngien masticateur dont le renouvellement dentaire était très probablement du même ordre que celui qui a été décrit chez des taxons actuels à régime alimentaire durophage : les Scaridae, les Tetraondontidae et le Carangidae *Trachinotus teraia*. Le gisement fossilifère qui a livré les plaques dentaires linguales de †*P. greenwoodi* renferme également d'abondants restes de mollusques (coquilles) et de macrocrustacés, ce qui laisse entrevoir la possibilité effective d'un régime durophage pour ce Notopteridae fossile.

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"Coalesced teeth"
Paleohistology

Osteichthyes are characterised by the presence of numerous odontodes closely related to the visceral skeleton in the pharyngeal cavity (Nelson, 1969; Lauder and Liem, 1983). In the Osteoglossomorpha (including the extant families Osteoglossidea, Mormyroidea and Notopteridae), there is a median lingual bony plate that rests on the three first basal skeletal elements of the branchial arches (Nelson, 1968). This bony plate supports numerous teeth (Taverne, 1972, 1977, 1978; Greenwood, 1973; Meunier and Brito, unpubl. data) and has an important function in the transfer of food from the buccal cavity to the esophagus (Kershaw, 1976; Sanford and Lauder, 1989, 1990).

†*Palaeonotopterus greenwoodi* Forey, 1997 is an extinct osteoglossomorph fish from the Albo-Cenomanian Kem-Kem Beds in southern Morocco. It is known by several articulated braincases (Forey, 1997; Taverne and Maisey, 1999; Cavin and Forey, 2001), and also by isolated visceral skeletal elements (Taverne, 2004), especially lingual tooth plates (Taverne, 2000; Cavin and Forey, 2001). These tooth plates are bulky and they do not show any teeth externally. Taverne (2000) described these plates as made by an unusual tubular tissue that he interpreted as "tubular bone", which appears

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to be inappropriate according to our preliminary observations. In fact, the lingual tooth plate of †*P. greenwoodi* likely resembles the pharyngeal jaw of the extant carangid shortfin pompano *Trachinotus teraia* Cuvier, 1832, notably when considering the morphology of the crushing surface (Meunier and Trébaol, 1987). In this paper, we present the results of our paleohistological study of the lingual tooth plate of †*P. greenwoodi* to elucidate its pattern and growth and we propose a correlative hypothesis on the diet of this Cretaceous teleostean fish.

MATERIAL AND METHODS

†*Palaeonotopterus greenwoodi*: one dental plate (PSA 34; Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris) from the Kem-Kem Beds, north-east of Taouz, Tafilalet Morocco, Upper Cretaceous. The plate was cleaned by taking off numerous attached grains of sand. It was used for the morphological description and for preparing ground sections.

The lingual dental plate was cut transversely to obtain two pieces (Fig. 1; *xy*); the anterior piece was cut longitudinally to obtain again two parts (Fig. 1; *ab*); the lower left one (*l*) was used for cross sections and the upper left one (*r*) was used for horizontal sections. The samples were embedded in polyester resin (GBS1; Brot). Transverse and horizontal sections were made with a sawing machine. The sections were grinded, polished and studied with an "Axiovert" microscope in natural transmitted and polarized light.

RESULTS

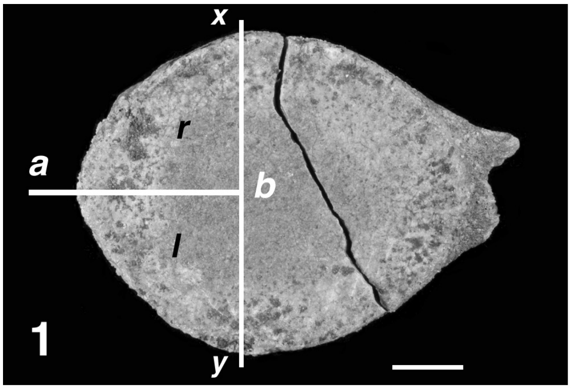
Morphological data

The lingual dental plate is approximately 12.5 mm thick and has an ovoid shape in occlusal view. Its upper surface is relatively homogenous, weakly concave and does not show any teeth (Fig. 1). The section ***xy*** looks heterogeneous and, at low magnification, it exhibits a more or less dominant tubular pattern (Fig. 2) that was ever pointed out by Taverne (2000). As it will be detailed by the histological examination (see below), five superimposed zones are distinguished (Fig. 3): (1) a compact crushing surface, (2) a dense zone where teeth are close to each other, (3) a zone where teeth are growing, (4) a dental cavity where odontogenesis takes place, and (5) a bony basal region.

Histological data

The tooth plate is made of numerous small teeth placed side by side (Figs 3-4). The teeth are 0.5-1 mm in width and 1-2 mm in height. Most teeth lie close to each other but some are separated by a thin amount of cellular bony tissue (Figs 5-9) that seems to have an adhesive function. In some cases the bony tissue between two teeth may be more abundant and contains small vascular canals, especially in the deepest part of the tooth plate (Fig. 7). The diameter and the number of the vascular canals progressively decrease from the dental cavity (Fig. 9) to the crushing surface where they are completely obliterated (Fig. 8). Each functional tooth is organised around a thin pulp cavity (Fig. 5) and is made of a cone of dentine that houses odontoblastic canaliculi (Fig. 8); the dentine shows a typical stratification (Figs 5-6). The teeth are not covered by any hypermineralized tissue. The bony tissue of the basis of the lingual dental plate is vascularised.

Figures 1-9. - *Palaeonotopterus greenwoodi* Forey, 1997. Lingual dental plate PSA 34.
Figure 1. - Superficial view of the gular dental plate. The anterior part is to the left. The ***xy*** axis indicates the cross section shown in Fig. 2. The axis ***ab*** indicates the two pieces respectively used for cross (***l***) and horizontal sections (***r***).
Figure 2. - General view of a cross section of the gular dental plate. Note the homogeneous crushing surface. The rectangle is enlarged in Fig. 3.
Figure 3. - Cross section. Detail of the various regions of the dental plate thickness (inset of Fig. 2). From top to bottom: (**a**) compact crushing surface; (**b**) dense zone of teeth; (**c**) zone of tooth growth; (**d**) odontogerous cavity; (**e**) bony basal region.
Figure 4. - Cross section. Detail of the dental cavity. Three young teeth (**1-3**) are visible at the bottom; the dentine is thin and the pulp cavity is wide. At the top, four other more advanced teeth (**4-7**) can be observed: the dentine is thicker and the teeth are longer.
Figure 5. - Cross section. Detail of the crushing surface of the dental plate (arrowheads) and of several adjacent teeth (**T**) separated by vascularised cellular bone (asterisk).
Figure 6. - Cross section. Detail of a young tooth in the vicinity of the dental cavity. Dentine (**De**) is clearly stratified. **PC** = pulp cavity.
Figure 7. - Cross section. Detail of cellular bone (asterisk) between teeth. It shows two vascular canals (arrows). The arrowheads point to osteocyte lacunae. **De** = tooth dentine.
Figure 8. - Horizontal section in the upper region of the lingual dental plate. The teeth are close to each other, and they look connected by thin patches of cellular bone (arrows); vascular canals are absent at this level.
Figure 9. - Horizontal section in a more basal region of the dental plate. The pulp cavities of the teeth are larger than those shown in Fig. 8. Relatively large areas are deprived of teeth and occupied by vascular canals (asterisks).
Scale bars: 1 = 1 cm; 2 = 5 mm; 3 = 1 mm; 4, 5, 9 = 200 μm; 6, 7, 8 = 100 μm.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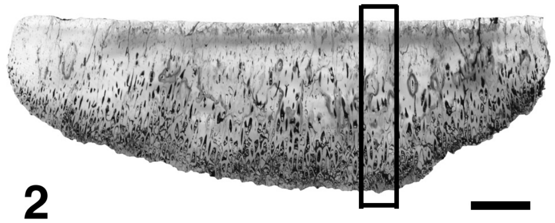
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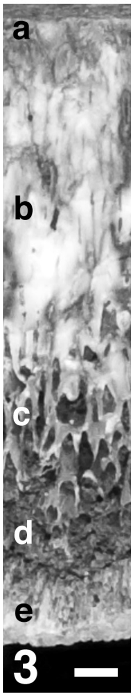
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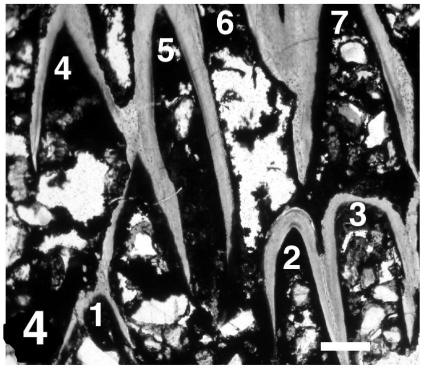
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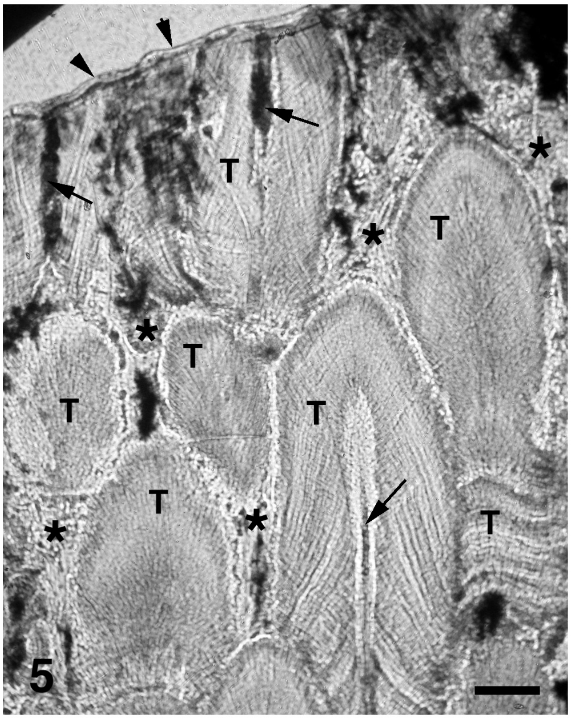
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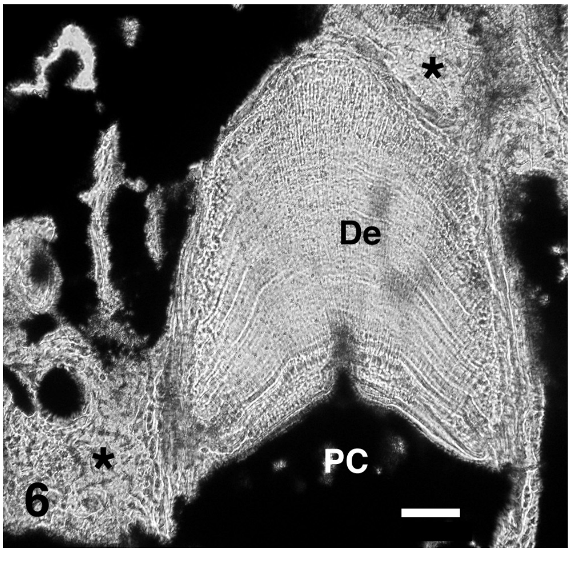
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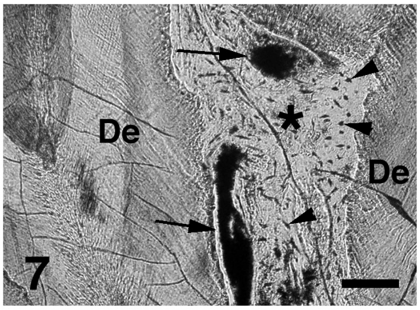
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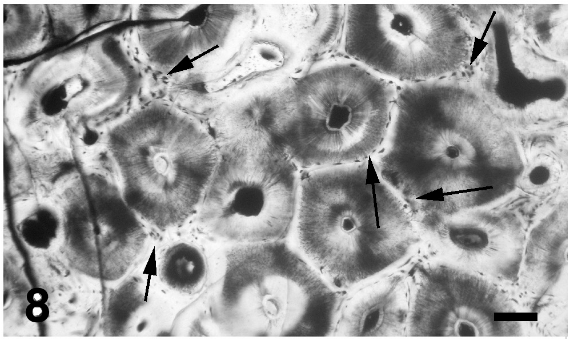
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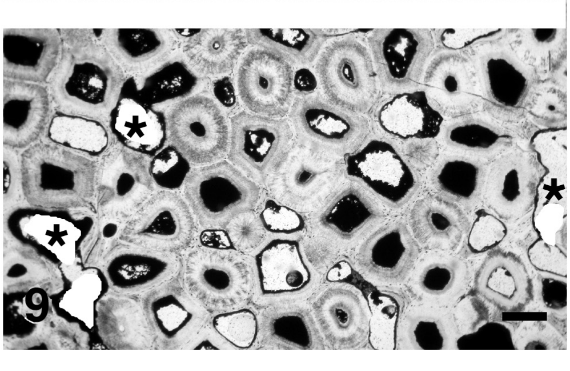
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DISCUSSION

The smallest teeth (with the thinnest layer of dentine) are in the deepest part of the tooth plate where there is a dentigerous cavity, and the well-developed teeth are located in the upper area of the plate. Therefore we assume that teeth appear in the deepest part of the lingual dental plate and then progress toward the abraded surface, when the dental plate grows. The ontogeny of the tooth plate is thus probably similar to the ontogeny of the "pharyngeal jaws" of the shortfin pompano *Trachinotus teraia*. In this latter species, the odontogenesis also takes place deep in the pharyngeal tooth plates (Francillon-Vieillot *et al*., 1994). Therefore, in †*Palaeonotopterus*, the pharyngeal epithelium would participate in the formation of teeth owing to long epithelial strands that penetrate in the depth of the tooth plate, as it was also demonstrated in the shortfin pompano (Francillon-Vieillot *et al*., 1994). When the teeth arrive at the occlusal surface, they are progressively worn down by repetitive crushing of prey. The most superficial teeth are replaced by new ones that were formed in the depth of the plate and have afterwards progressed towards the crushing surface. Such a progressive replacement of successive tooth generations is known in various other teleostean taxa (Britski *et al*., 1985; Meunier and Trébaol, 1987), and has been experimentally confirmed with vital labelling in *Trachinotus teraia* (Trébaol *et al.,* 1991) and with an autoradiographic study in the tetraodontid fish *Sphoeroides greeleyi* (Andreucci *et al*., 1982).

Altogether, with strictly contiguous teeth, the dental plate of †*Palaeonotopterus* resembles the "coalesced teeth" of the jaws of tetraodontid fish (Andreucci, 1968; Britski *et al*., 1985) and of the shortfin pompano, a modern carangid fish (Trébaol *et al*., 1991; Francillon-Vieillot *et al*., 1994). However, contrary to the pompano that has a low density of teeth, the abraded surface of †*Palaeonotopterus*' dental plate is virtually constituted of teeth only. In the pompano it is constituted of both teeth and a substantial amount of acellular bone (Meunier and Trébaol, 1987).

The similar structural organisation of the lingual dental plate of †*Palaeonotopterus*, with tetraodontid (Andreucci, 1968; Britski *et al*., 1985) and scarid jaws (Boas, 1879) supports the hypothesis that †*Palaeonotopterus* was a durophagous fish. Moreover, the fossiliferous beds where the lingual dental plates were collected have also delivered fossil shells, including molluscs and crustaceans (Dutheil, unpubl. data), which could have constituted an important part of the diet of †*Palaeonotopterus greenwoodi*.

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